Pedobiologia, Bd. 9, S. 93—98 (1969)

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Did lumbricids survive the quarternary glaciations in Norway?

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With one figure

(Received 14. 6. 1968)

1. The ancient explanation

After the appearance of the theory about the Quaternary glaciations, Scandinavian scientists imagined that an enormous ice mantle covered the entire Scandinavian Peninsula, from the high mountains to the outmost skerries, and that all life, animal as well as plant, was exterminated. They thought that during each interglacial the organisms had to reconquer the Scandinavian countries by invasion from the tundra-like regions in Central Europe, where they were supposed to have survived.

2. Germ of a new theory

Before 1900 the Norwegian botanist Axel Blytt (1893) had already called attention to a group of plants living in the Scandinavian high mountains, but lacking in the rest of Europe and in western Siberia, and which consequently cannot have invaded Scandinavia from the south or east. On the other hand, they are found in Greenland and North America, some even in eastern Siberia. Blytt imagined their immigration by a land-bridge from Greenland through Iceland and the Faeroe Islands to western Norway (and Scotland). He even suggests that perhaps some plants may have survived one or more of the glaciations in Norway.

The climate during the last interglacial is quite well known. Animal and vegetable life in Scandinavia was then evidently richer than now. The theory of survival is supported also by the fact that fossils of mountain plants are found in southern, but not in central Sweden. In central Sweden the glacier retired very rapidly, evidently as a consequence of a radical improvement in climate, which allowed forest plants to follow the ice edge. It seems that tundra plants did not reach the northern parts of Sweden from the south. That a branch of the sea extended through central Sweden, was certainly also a contributing factor.

The Norwegian geologist Thorolf Vogt (1912) showed that the outmost small clusters of islands, Røst and Værø, of the Lofoten island chain, were not glaciated during the last glacial, and have perhaps never been covered with ice.

3. Two separate refuges

The Swedish botanist Thore C. E. Fries (1913) divided the mountain plants into several geographical groups. One of his groups consists of the "ubiquitous" species, showing a comparatively continuous distribution through the Scandinavian mountain region. But some other species showed concentrations in two mountain regions, like two widely separated "islands" in the mountains, one in southern and one in northern Norway (Fig. 1). In the remaining parts of the mountains the vegetation is much less rich in

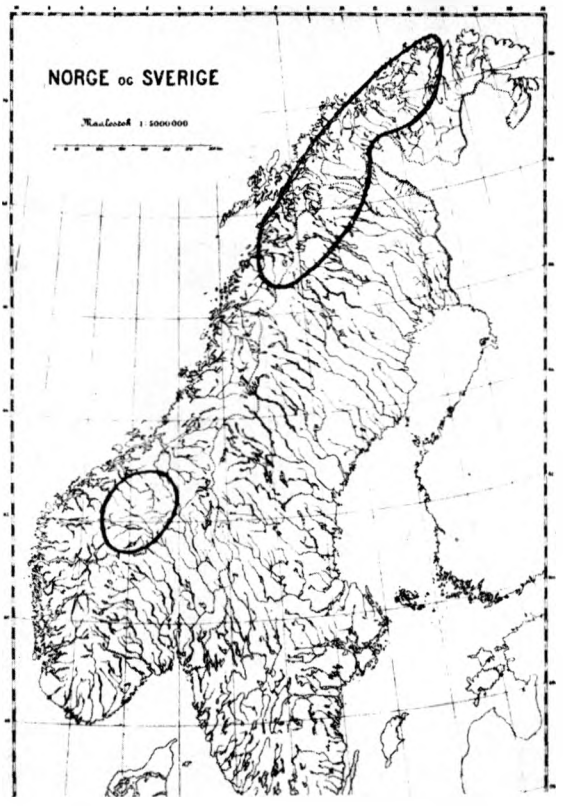

Fig. 1. The two "island" regions in the Scandinavian high mountains.

species, both north and south of the "islands", as well as between them. Many of the rare mountain species are found in both "island" regions, others only in either the northern or the southern region.

In the two "island" regions plants belonging to other geographical groups concentrate as well. In the northern region lives for instance the orchid *Platanthera parvula*, whose nearest locality outside Norway is near Yenissey in Siberia, and *Oxytropis deflexa*, which has not been found nearer than in the Baikal region. In the southern region we find *Artemisia norvegica*, occurring only there and in Ural, and *Taraxacum dovrense*, whose nearest relative is found in the Alps. If these were not glacial survivors, it would be very difficult, or impossible, to explain such a discontinuous distribution (Nordhagen 1947).

The abundance of species in the southern region may be explained by supposing an icefree coastal strip, a refuge, in southern Norway, where the plants could survive the last glaciation. When the ice began to retire eastwards, the plants followed. On the coastal strip other species immigrated when the climate improved.

It has been proposed that plants could perhaps have survived as well on nunataks, i. e. mountain peaks projecting from the ice, but such localities were probably too small to allow survival.

The abundance of species in the northern region may be explained in a similar way. But as the region is of much greater extent and has a more abundant vegetation than the southern, one may suppose that the icefree coastal strip in northern Norway was

considerably longer, and in some places also broader, than in the southwest. As to the ubiquitous mountain plants, they are fairly modest and have good facilities for spreading. Many of them may probably have survived on the refuges and afterwards spread in all directions.

As the botanists had now pointed out the problem, zoologists also began to interest themselves in it. Ekman (1920) called attention to a small Fenno-scandian rodent, the lemming (*Lemmus lemmus*), whose nearest relatives are found near the river Ob in Siberia. He is of the opinion that the Scandinavian species had developed by geographical isolation caused by the glacier and survived at least the last (Würm) glaciation on Norwegian refuges. Other zoologists, e. g. Lindroth (1939), Natvig (1948), could show similar phenomena in insects. It became obvious that even among animals of the Scandinavian high mountains there are species with a discontinuous distribution like that of many of the plants.

4. Extent of ice free areas

The question about the existence of ice free areas along the coasts of the Northern Atlantic is of fundamental importance for the interpretation of the distribution and history of plants and animals. Zoologists and botanists ordinarily agree that refuges existed in Scandinavia, but as to the western side of the Atlantic, e. g. Labrador, opinions are more divergent. Geologists generally agree as to the southern limitation of the maximal glaciation in Europe and America during each of the two last Quaternary glaciations, but as to the areas north of the southern limitation along the Atlantic coasts opinions diverge. Some geologists are of the opinion that ice free areas did not exist, at least not large enough to permit survival of a considerable number of plants and animals. Other geologists think that parts of Ireland, Scotland, western and northern Norway, Bear Island, Spitzbergen, Iceland, Greenland, Labrador, Newfoundland, Gaspé and Nova Scotia were not completely covered with ice during the last or earlier glaciations. The Norwegian botanist and geologist Eilif Dahl (1946) tried to show, by means of the physical properties of ice, that a coast with the topography we find in western and northern Norway and in Greenland, with high mountains near deep sea, cannot have been covered with a continuous ice mantle.

5. Endemic and peregrine species

In the Alps the glaciations were evidently not complete. The refuges there are characterized by a high percentage of endemic species. Many of them evidently appeared because of geographical isolation during various periods. In North America there is evidence of accumulation of endemics in the supposed refuges e. g. in Newfoundland. Nordhagen a. o. have discovered endemic plant species in Scandinavia, whose nearest relatives are found e. g. in Switzerland. Lindroth asserts that several Icelandic insects survived at least the last glaciation there. Recently Omodeo (1963) asserts that most of the Oligochaeta of Iceland and Greenland survived the last, and probably all of the Quaternary glaciations, *in situ*. In fact, around the northern Atlantic, species of plants and animals live which are found nowhere else on earth. They have without doubt differentiated there during the Quaternary and have survived at least the last glaciation e. g. in Scandinavia.

If we accept that organisms survived one or several glaciations in refuges, we still do not know how and when the Greenlandic-American species, the East-Siberian and the Central-European species arrived in Scandinavia. It is not difficult to imagine that some species could immigrate from Siberia or Central Europe into Scandinavia, e. g. during the last interglacial, but the species common to Scandinavia, Greenland and North America demand the existence of land-bridges, and such land-bridges have certainly not existed as late as during the last interglacial. Consequently these species must have survived at least the two last glaciations in Scandinavia.

6. The contribution of the Lumbricids. Peregrine and endemic species

Working on the Norwegian Lumbricids I found 18 species of the family in our country, and I became interested in the question whether any of them have possibly survived one or more of the glaciations in Scandinavia.

Many species of Lumbricids show a great adaptability to new ecological circumstances, and therefore become easily spread over great parts of the world, actively or passively. They are peregrine species. Other species do not show such adaptability to alien circumstances, and if they, by chance, become transported into foreign regions, they will soon die out. They are endemic species with a clearly limited distribution. The region where we find endemic Lumbricids, extends from south-eastern U. S. A. through southern and central Europe with North Africa, through Caucasia to Japan. Probably even great parts of central Asia belong to the region of endemic Lumbricids, but those areas still remain insufficiently investigated.

The southern limit of the zone of endemic Lumbricids is formed mainly by water and deserts, which the Lumbricids cannot easily pass. The northern limit conforms surprisingly well with the southern limitation of the greatest extension of the Quaternary glaciation, at least in Europe and North America, where the circumstances are best known. North of that line are found mainly peregrine or ubiquitous species. It is no wonder that it was long supposed that the Lumbricids were exterminated during the glaciations and had to reconquer these regions after each glaciation. However, as I have already mentioned, Omodeo is of the opinion that the Lumbricids have survived the Quaternary glaciations in Iceland and Greenland. Why not even in Norway?

7. Ecological factors

Along the Norwegian coast the summer is comparatively cool, but because of the Gulf Stream the winter climate is very mild. Moreover the high, steep mountains along deep, long fjords cause an extremely high precipitation, so that western Norway forms topographically and climatologically a very peculiar region in Europe. Studying the ecological factors regulating the distribution of Lumbricids, one must pay attention also to the continuous mountainous chain extending along the whole of the Scandinavian Peninsula.

It is difficult to say how much these factors influence the distribution of the Lumbricids, because our knowledge about the ecological factors deciding the distribution is still very deficient; but it seems probable to suppose that the mentioned factors together will not promote the distribution. Further we have to notice the influence of human culture. Julin (1949) divides the Lumbricids into 4 groups, viz. (1) *hemerophiles*, which are favoured by culture, (2) *hemerophobes*, which are averse to culture, (3) *hemerodiaphores*, which are indifferent to the influence of culture, and (4) *hemerobionts*, which are entirely dependent on culture. — For our problem mainly the 2nd and 3rd groups are of interest.

Evidently nothing prevents the supposition that Lumbricids were widely distributed in the Palaearctic region during the Tertiary. Omodeo (1963) underlines the very slow evolution of the terrestrial Oligochaets, and their high adaptability makes it difficult to imagine climatic changes which can completely exterminate a genus or family of worms living in a continent.

8. *Dendrobaena norvegica*

Julin (1949) calls attention to one species, *Dendrobaena norvegica* (Eisen), which is found in northern and southern Norway, near the two regions of supposed refuges, and he compares its distribution with that of two plants, considered as glacial survivors. Later on Omodeo (1957) reports that form from Greenland. I have now obtained from

Denmark material of Greenlandic Lumbricids, which proved to contain but two species, one of them being precisely *D. norvegica*, which evidently is rather widely distributed in Greenland.

The Danish zoologist VIBE (1956) says that "The study of the landfauna of Greenland shows more and more clearly that we have to deal with the remnants of an old fauna, which had a more or less circumpolar distribution before the glacial period, but which later on became confined to isolated localities distributed over the boreal and arctic area."

D. norvegica is evidently a hardy species, living at great heights in the Norwegian mountains. It is found exactly in the two Norwegian refuge regions and in Greenland, but it is not with certainty reported from any other part of the world. It is capable of survival under arctic conditions, and I am of the opinion that it supports beautifully the theory about glacial refuges in Norway and in Greenland.

9. Other species

From southwestern Greenland only one more species is known with certainty, viz. *D. octaëdra* (SAVIGNY). It belongs to the ubiquitous species, and accordingly its distribution does not tell anything about eventual survival or immigration into Scandinavia; but it is the most hardy of all Lumbricids, found even in Novaya Zemlya. It has good spreading abilities, and it avoids cultivated soil. Perhaps it has partly survived in refuges, partly immigrated in postglacial time.

A third species has also been found near the northern Norwegian refuges, viz. *Eiseniella tetraëdra* (SAVIGNY), but it has been found in central and southeastern Norway as well, and is widely distributed in Sweden. Because of its small size and its aquatic habitat it has probably often been overlooked, and may have a much wider distribution in Norway. Because of its hardiness it is difficult to exclude it from the possible survivors. Undoubtedly there existed small rivulets or brooks flowing through the refuges during summer. On the other hand this species has never been reported from Greenland.

Finally the distribution of *D. tenuis* (EISEN) seems to indicate a western immigrant. It is widely distributed in North America, Britain and Central Europe, but has only occasionally been reported from Denmark and Sweden. It is really difficult to imagine an overseas distribution of a Lumbricid, but its existence in the small island Grimsey north of Iceland may indicate such an overseas distribution. On the other hand it has not been found in the mainland of Iceland. However, there may be even another explanation, viz. that it has survived on south Norwegian (and Icelandic?) refuges, from where it has spread through southern Norway, but has not yet reached Sweden. At any rate, it is no true southern immigrant in Norway.

The remaining Norwegian Lumbricids seem to be southern immigrants. Their known distribution in Sweden and Finland excludes the probability of immigration from the northeast for any of them. Only if *D. octaëdra* is to be considered as partly immigrated, may it have arrived by that route also.

10. Resumo

En la pasinta jarcento oni imagis ke dum la kvaternaraj glaciperiodoj grandega glacio komplete kovris Skandinavion. Poste norvegaj botanikistoj konstatis ke kelkaj plantoj vivas nur en du "insulformaj" regionoj en la norvega altmontaro (Fig. 1), kaj cetere nur en Norda Ameriko, Groenlando, la Alpoj kaj orienta Siberio. Oni interpretis tion kiel pruvon ke ili travivis la glaciperiodojn sur senglaciaj areoj de la norvega marbordo. Zoologoj konstatis similajn fenomenojn, precipe inter insektoj. La autoro montras ke simile la distribuo de kelkaj specioj de Lumbrikedoj estas klarigebla nur per akcepto de la teorio pri senglaciaj marbordaj areoj. Vidu cetere lian artikolon en Scienca Revuo **16**, 57—67, 1966.

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